

## Ecological Studies of Hawaiian *Metrosideros* in a Successional Context<sup>1</sup>

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**ABSTRACT:** 'Ōhi'a (*Metrosideros polymorpha*) is the dominant rain forest tree species in Hawai'i. It has long impressed botanists for its morphological variability and ecological amplitude. The present study has documented differences in the distribution of *Metrosideros polymorpha* varieties in populations of 'ōhi'a growing on adjacent young and old flows. Pubescent varieties are present on young volcanic substrates, but tend to be absent from older soils in the rain forest zone. The genetic basis for these varieties has been confirmed in a common garden experiment. The water relations of pioneer and older forest 'ōhi'a have been examined and shown to differ, so that the pioneer 'ōhi'a tend to be able to maintain turgor at lower relative water contents than the glabrous varieties.

THE DOMINANT RAIN FOREST TREE throughout the Hawaiian archipelago is 'ōhi'a (*Metrosideros polymorpha*, Myrtaceae). By the early 1970s a widespread dieback of 'ōhi'a forest stands on the island of Hawai'i had become so noticeable that studies were initiated to describe and determine its causes (Mueller-Dombois 1974, 1980, Mueller-Dombois et al. 1980, USDA Forest Service 1981). When aerial photographs taken in 1954, 1965, and 1972 of an 80,000-ha area were examined, it was reported that the area of severe decline, with over 40% of the tree canopy dead or dying, had increased from 120 ha in 1954 to 34,500 ha in 1972 (Petty, Burgan, and Nelson 1975). It was postulated that this was caused by a disease that would spread and eventually eliminate much of the native 'ōhi'a rain forest. However, systematic studies of permanent plots established in the dieback area indicated that abundant regeneration was associated with dieback stands (Jacobi, Gerrish, and Mueller-Dombois, this issue; Mueller-Dombois et al. 1980). These studies followed an earlier hypothesis by Mueller-Dombois (1974) that the decline was a

natural successional phenomenon rather than a new disease.

Initial support for this hypothesis came from several sources. Considerable research had focused on identifying fungal and insect agents believed to be causative agents in the decline. While the root rot fungus, *Phytophthora cinnamomi*, and the grubs of a native cerambycid beetle, *Plagithmysus bilineatus*, were often associated with dying trees and could hasten the death of weakened trees, neither could be considered primarily responsible for initiating decline (Hwang 1977, Papp et al. 1979). Further evidence was presented by the literature describing a similar large-scale canopy decline that occurred around the turn of the century on the island of Maui (Lewton-Brain 1909, Lyon 1909). Despite this earlier dieback, *Metrosideros* persists in that area today.

Following the recognition of the dieback as a natural successional phenomenon where dieback stands were usually associated with abundant regeneration, Mueller-Dombois hypothesized that one physiological ecotype of 'ōhi'a might be replacing another in a successional sequence (Mueller-Dombois et al. 1980). Stimulus for this hypothesis came in part from the observation in one of the permanent plots that most of the regeneration appeared to be a glabrous-leaved variety of *Metrosideros*, while the declining canopy

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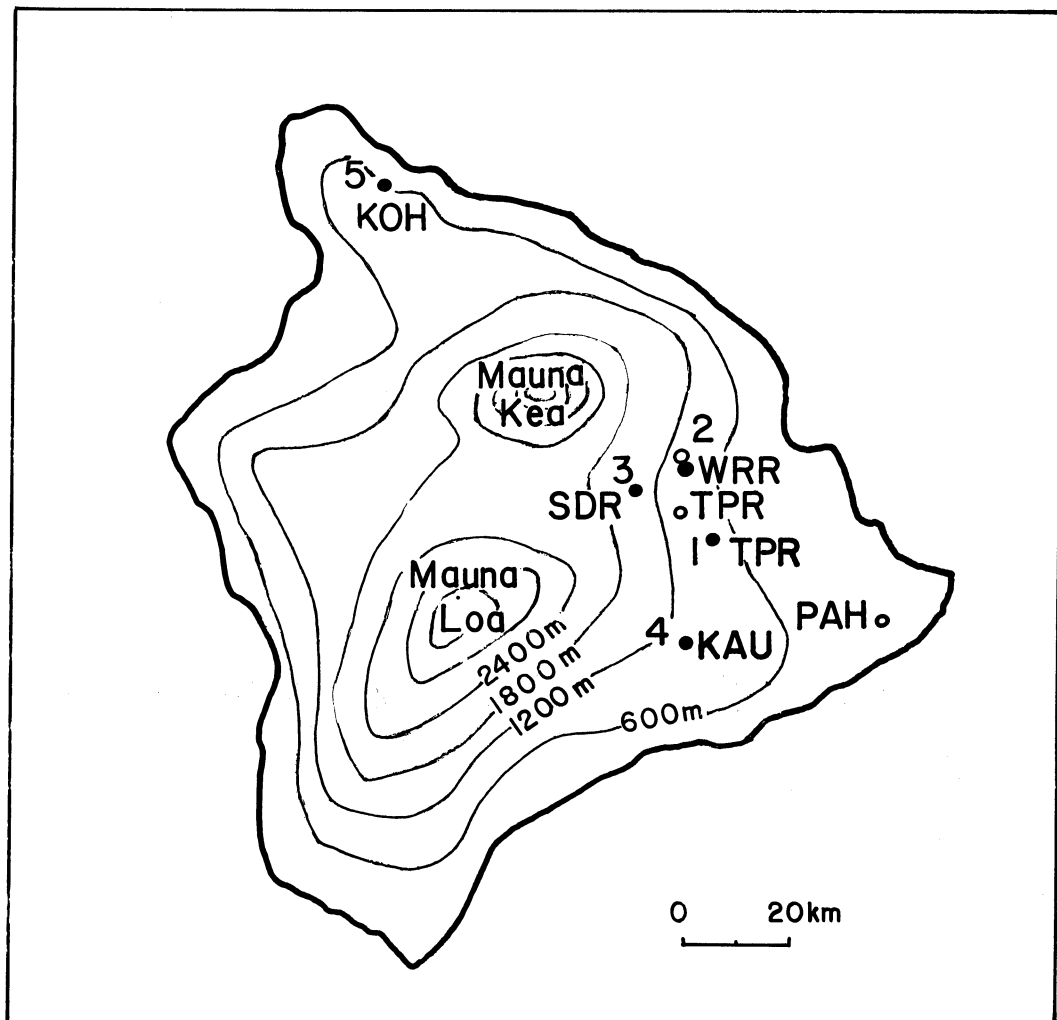


FIGURE 1. Island of Hawai'i showing locations of paired sites on young and old flows where the distribution of *Metrosideros* varieties were compared (open circles), and locations of parental populations for seeds planted on the experimental tanks (solid circles with numbers). TPR = Tree Planting Road; WRR = Wailuku River Road; SDR = Saddle Road; KAU = Ka'ū Desert; KOH = Kohala; PAH = Pāhoa.

trees were mostly of a pubescent-leaved variety. Other observations indicated a greater percentage of pubescent 'ōhi'a saplings in pioneer situations, such as on young lava flows and in disturbed areas along roadsides, than in the surrounding older forest, which was dominated by a glabrous 'ōhi'a variety.

Some workers have recognized six *Metrosideros* species from the Hawaiian archipelago. Of these, five are endemics of peculiar

morphology and limited distribution. What has been considered as the sixth, *M. polymorpha*, along with its approximately 23 infraspecific taxa, is by far the most widely distributed, being found from sea level to 2500 m (8200 ft), and from recent, sparsely vegetated flows on the island of Hawai'i, to rain forests and open bogs on most of the high Hawaiian islands (Rock 1917, Skottsberg 1936, 1944). Some of the considerable morphological variation that occurs among

TABLE 1  
ADJACENT YOUNG AND OLD SITES SAMPLED TO DETERMINE 'ŌHI'A VARIETY DISTRIBUTION

LOCATION AND AGE*	ELEVATION (m)	MEAN ANNUAL PRECIPITATION†	SUBSTRATE	VEGETATION
Tree Planting Road 1881 flow	1,160	3,500–4,000	Pāhoehoe with shallow soil	Open-canopied 'ōhi'a scrub forest to 6 m tall; much exposed lava
800 B.P. ± 200 yr			'A'ā with shallow soil	Closed-canopied 'ōhi'a forest to 19 m tall with native understory and tree ferns
Wailuku River Road 1855 flow	1,112	4,000–5,000	Pāhoehoe with shallow soil	Open-canopied 'ōhi'a scrub forest to 6 m tall; some exposed lava
3500 B.P. ± 300 yr			Shallow poorly drained soil on pāhoehoe	Open-canopied 'ōhi'a forest to 15+ m with dead snags; understory of <i>Dicranopteris</i> fern mats
Pāhoa 1955 flow	275	2,500–3,000	'A'ā	Open-canopied 'ōhi'a scrub to 5 m tall; few other species except <i>Stereocaulon</i> lichen
1790 flow	305		'A'ā with shallow soil	Closed-canopied 'ōhi'a forest to 20 m tall with native and exotic understory

\*J. Lockwood and R. Moore (personal communications).

†DLNR (1970).

various *Metrosideros* populations has been shown to be of clinal nature related to climatic and elevational gradients (Corn 1979, Corn and Hiesey 1973). The present study has examined differences in *Metrosideros* populations that can be related to a successional sequence.

#### THE FIELD SURVEY

Several avenues of research have been undertaken to determine whether there is a successional replacement of certain 'ōhi'a taxa by others, and to investigate physiological characteristics of the various 'ōhi'a that could be related to their successional position. The mosaic character of differently aged flows on the slopes of the young Hawaiian shield volcanoes provides an excellent lab-

oratory for the study of vegetation succession and community development. Where differently aged flows occur within short distances of each other, the effects of substrate age and character on forest development can be compared under similar climatic conditions. Three sites were chosen where the distribution of varieties of 'ōhi'a were compared on adjacent young and old sites (Figure 1, Table 1) using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974).

At each location pubescent varieties of 'ōhi'a are abundant on the young sites and less abundant, or absent, on the older sites (Figure 2). At the low-elevation site (Pāhoa), the pubescent 'ōhi'a is *M. polymorpha* var. *incana*, while at higher elevations it is *M. polymorpha* var. *polymorpha* with apparent intergrading forms between the two at mid-

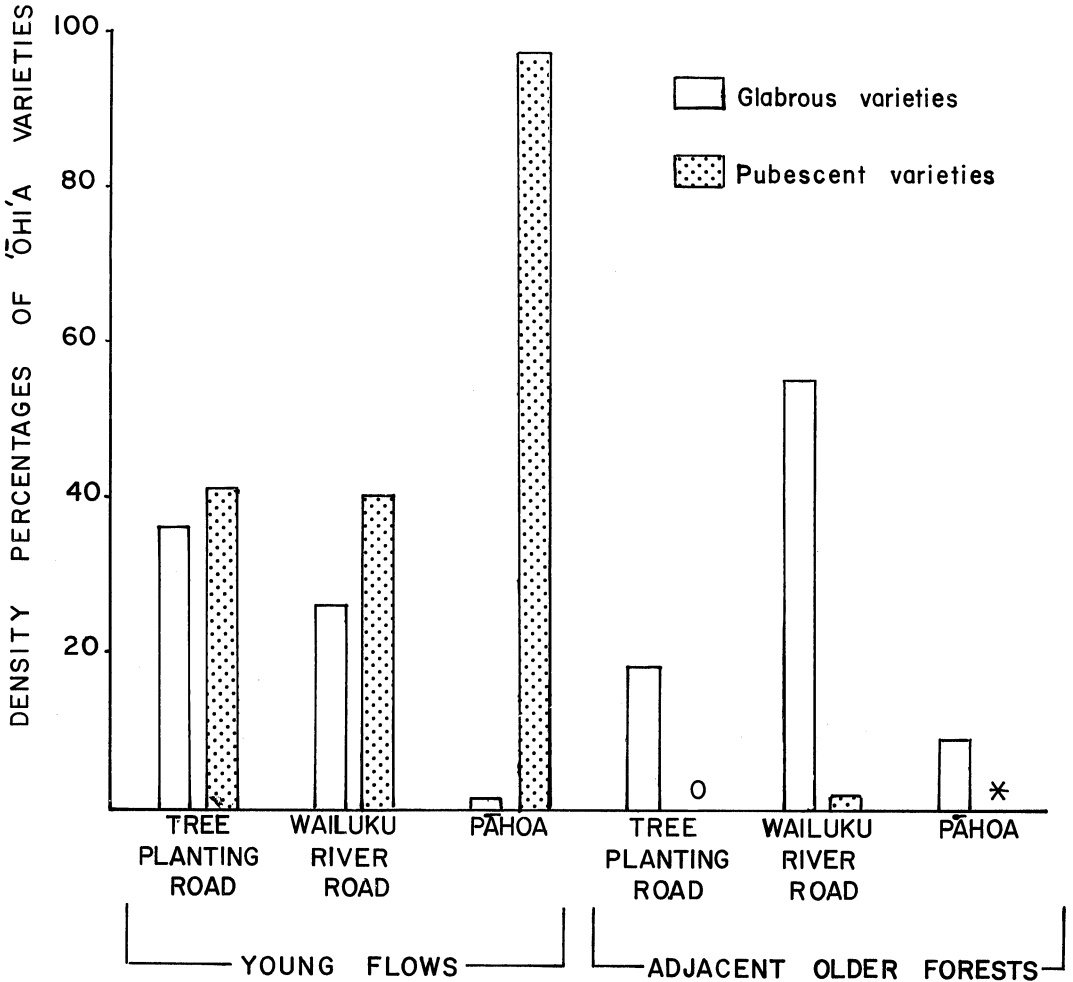


FIGURE 2. Percent of total stand density for pubescent and glabrous *Metrosideros* varieties at three sites where pioneer communities were compared with older forest stands (see Table 1). At the Tree Planting Road and Wailuku River Road sites, the pubescent variety is mostly *M. polymorpha* var. *polymorpha*, and the glabrous variety mostly *M. polymorpha* var. *glaberrima*. At the Pāhoa site, the pubescent 'ōhi'a is *M. polymorpha* var. *incana*, and the glabrous 'ōhi'a is *M. polymorpha* var. *macrophylla*. Note the virtual absence of pubescent 'ōhi'a from the older forest sites. \*Present but not recorded during sampling.

elevations. The glabrous varieties include *M. polymorpha* var. *macrophylla* and *M. polymorpha* var. *glaberrima*, which again intergrade.

A rain forest laden with bryophytes and with a moist organic soil appears wetter than a seemingly desertlike, barren, or sparsely vegetated recent lava flow, even though the two may be juxtaposed as they often are on the slopes of Mauna Loa and Kīlauea on the volcanically young island of Hawai'i. Since

water availability is one of the most obvious differences between barren young lava flows and forested older flows, several aspects of the water relations of various 'ōhi'a populations were examined.

#### THE TRANSPLANT EXPERIMENT

The growth response of five 'ōhi'a populations to a gradient of depth to water table has

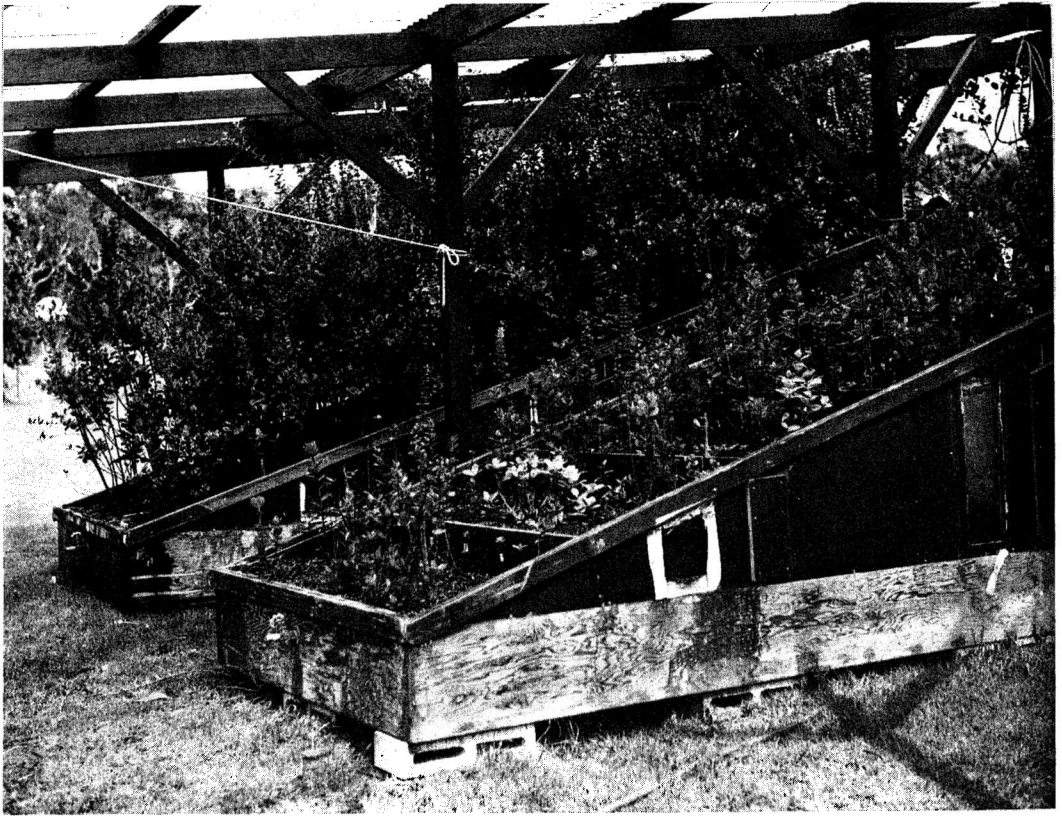


FIGURE 3. The two experimental tanks with a fixed water table at 15 cm height. This photograph was taken when seedlings were  $2\frac{1}{2}$  yr old. The substrate in the foreground tank is cinder; the substrate in the rear tank is soil.

been examined using two tanks simulating soil wedges and with a permanent water table modified after Mueller-Dombois (1963, 1964) and Mueller-Dombois and Sims (1966). Each tank measures 4.9 m (16 ft) long and 1.5 m (5 ft) wide, with the gradient of depth to water table produced by eight levels on each tank (Figure 3). One of the tanks was filled with recent volcanic cinder and the other with a forest soil derived from fine-textured eutrophic ash. The tanks were planted with seed from morphologically homogeneous populations growing on sites of different ages (Table 2). On each tank, seeds of two parents for each of the five test populations were planted in carefully predetermined locations on each level. Seedlings were surface-watered for  $1\frac{3}{4}$  yr, after which only groundwater was provided. This was fed

by slowly dripping water through a pipe mounted inside the high-end wall and ending 10 cm above the bottom in each tank. The inflow drip was adjusted to the outflow drip at the low end of each tank, where a tap was mounted at 15 cm height.

After  $1\frac{1}{2}$  yr of growth, significant differences between levels had not been demonstrated, but statistically significant morphological differences were recorded among the varieties (Table 3). This confirms the genetic basis for the varieties that replace each other in different stages of soil development along a primary successional gradient. Evidence of ecotypic differentiation along elevational and climatic gradients had previously been documented (Corn 1979, Corn and Hiesey 1973). Only now, however, has ecotypic differentiation been reported to be associated with

TABLE 2  
SITE DESCRIPTIONS FOR SOURCES OF SEEDS PLANTED IN EXPERIMENTAL TANKS

POPULATION AND LOCATION	ELEVATION (m)	MEAN ANNUAL PRECIPITATION* (mm)	SUBSTRATE AND AGE <sup>†</sup>	VEGETATION
1. <i>M. polymorpha</i> var. <i>macrophylla</i> Tree Planting Road plot 27, <sup>‡</sup> Waiākea Forest Reserve	896	3,800–5,000	Shallow soil on pāhoehoe; c. 1500 B.P.	Closed-canopy forest to 17 m; native shrub understory
2. <i>M. polymorpha</i> var. <i>glaberrima</i> Near Wailuku River plot 17, Hilo Forest Reserve	1,137	6,350–7,620	Deep, weathered ash; older than 3000 yr	Forest surrounding open- canopied bog; 'ōhi'a to 10 m tall
3. <i>M. polymorpha</i> var. <i>polymorpha</i> 'A'a flow near Saddle Road plot 14, Upper Waiākea Forest Reserve	1,530	3,175–3,810	Recent 'a'a; 1855 flow	Open-canopy scrub forest to 6 m with much exposed lava
4. <i>M. polymorpha</i> var. <i>incana</i> Ka'u Desert, Hawaii Volcanoes National Park	914	1,270–1,905	'A'a; c. 250 B.P.	Open-canopy scrub forest to 6 m with much exposed lava
5. <i>M. polymorpha</i> var. <i>glaberrima</i> Kohala Forest Reserve	1,219	3,810–4,450	Wet, weathered ash; 0.06–0.25 million years	Low 'ōhi'a scrub forest 2– 8 m tall with bryophytes

\*DLNR (1970).

<sup>†</sup>J. Lockwood (personal communication), McDougall and Swanson (1972).

<sup>‡</sup>Mueller-Dombois et al. (1980).

TABLE 3

CHARACTERS OF PROGENY OF FIVE *Metrosideros polymorpha* POPULATIONS GROWN FOR 1½ YR IN TWO EXPERIMENTAL TANKS

POPULATION NO. AND TANK	HEIGHT (cm)	LENGTH OF LEAF (mm)	WIDTH OF LEAF (mm)	PETIOLE LENGTH (mm)	DIAMETER OF STEM (mm)	LEAF SHAPE	LEAF APEX SHAPE	LEAF BASE SHAPE	PUBESCENCE
1. Soil	23.12	51.65	35.80	4.07	4.02	Obovate	Acute to rounded	Acute	Glabrous
Cinder	19.76	48.42	332.58	3.54	5.15				
TOTAL	21.76C	50.77A	34.92A	3.92B	4.34C				
2. Soil	14.52	43.03	30.30	2.53	4.38	Elliptic to obovate	Acute to rounded	Acute	Glabrous
Cinder	7.83	39.50	27.67	2.00	4.67				
TOTAL	12.35D	45.52C	29.93B	2.45D	4.42C				
3. Soil	32.74	33.02	30.88	2.21	5.09	Orbicular, ovate to elliptic	Rounded to retuse	Cordate	Wooly
Cinder	17.45	34.14	28.22	2.27	5.35				
TOTAL	25.39B	33.36D	30.07B	2.23D	5.17B				
4. Soil	49.32	48.40	35.81	3.31	6.17	Ovate	Acute	Rounded	Short- tomentose
Cinder	30.48	44.17	30.40	2.87	6.83				
TOTAL	41.28A	46.78B	33.75A	3.14C	6.42A				
5. Soil	16.25	48.25	35.48	4.77	4.30	Obovate	Obtuse to rounded	Acute	Glabrous
Cinder	10.75	45.00	33.70	3.80	5.22				
TOTAL	14.63D	47.69AB	35.17A	4.60A	4.45C				

NOTE: See Table 2 for descriptions of populations by number. Means for characters in columns based on population totals followed by the same letter are not significantly different using Duncan's multiple range test.

TABLE 4

PERCENTAGE ESTABLISHMENT OF PROGENY OF FIVE *Metrosideros polymorpha* POPULATIONS GROWN FOR 1 YR  
IN TWO EXPERIMENTAL TANKS

POPULATION	SOIL	CINDER	TOTAL
1. <i>M. polymorpha</i> var. <i>macrophylla</i>	51.9	33.8	42.8
2. <i>M. polymorpha</i> var. <i>glaberrima</i>	51.9	29.4	40.6
5. <i>M. polymorpha</i> var. <i>glaberrima</i>	54.4	26.9	37.5
ALL GLABROUS	52.7	30.0	40.3
3. <i>M. polymorpha</i> var. <i>polymorpha</i>	75.0	52.2	63.7
4. <i>M. polymorpha</i> var. <i>incana</i>	76.9	51.2	64.1
ALL PUBESCENT	75.9	51.9	63.9

NOTE: See Table 2 for descriptions of populations by number. Total possible *N* per population per substrate = 320.

edaphic differences related to substrate age within a common elevational belt.

The marked effect of substrate type on the growth and establishment of the different varieties should be noted. With the exception of basal diameter, sizes of plant characters measured were larger on plants grown on the tank filled with soil derived from eutrophic ash. Further, far more plants of all populations became established on the soil tank, though the two pubescent varieties were more successful on both tanks. Since the pubescent varieties represent pioneer populations, one might expect them to exhibit the best initial success on newly exposed substrates such as those provided on the tanks (Table 4). The tanks will be dismantled at the end of the experiment to determine how the water table has affected the rooting patterns of the different varieties.

#### STUDY OF PLANT-WATER RELATIONS

Having determined that the two pubescent varieties do behave as pioneers in the field and are more successful than the glabrous varieties in becoming established on exposed substrates, studies of tissue-water relations have been conducted in an attempt to establish the physiological basis for the observed distributions. This was done using the pressure-volume curve technique, which entails repeated determination of water potential from a branch starting at full saturation until 40–50% of total water at

saturation has been lost (Scholander et al. 1965, Tyree and Hammel 1972). Water potential is measured with a pressure chamber, and branches are weighed at the time of water potential measurement so that relative water content can be determined. When a plot is drawn of the inverse of the water potential versus relative water content (pressure being inversely related to volume), a graph similar to Figure 4 results.

The components of plant water potential can be partitioned out from total plant water potential. Total plant water potential is considered to be the sum of turgor pressure plus osmotic potential plus matric potential. The latter is usually considered insignificant. The extrapolation of the linear portion of the curve of inverse water potential versus relative water content to the *y* axis provides an estimate of the osmotic potential at full turgor. The *x* intercept (which falls to the right of the scale illustrated in Figure 4) of the linear portion of the curve is an estimate of the apoplasmic water content. The difference between the line defining osmotic potential and the curve then gives an estimate of turgor at any given relative water content.

Plotting turgor versus relative water content permits a comparison of the ability of different plants to maintain turgor (Figure 5). The bulk modulus of elasticity *E* is a function of the slope of this curve near saturation and is calculated as

$$E = \frac{\Delta P}{\Delta RWC} (\overline{RWC} - A)$$



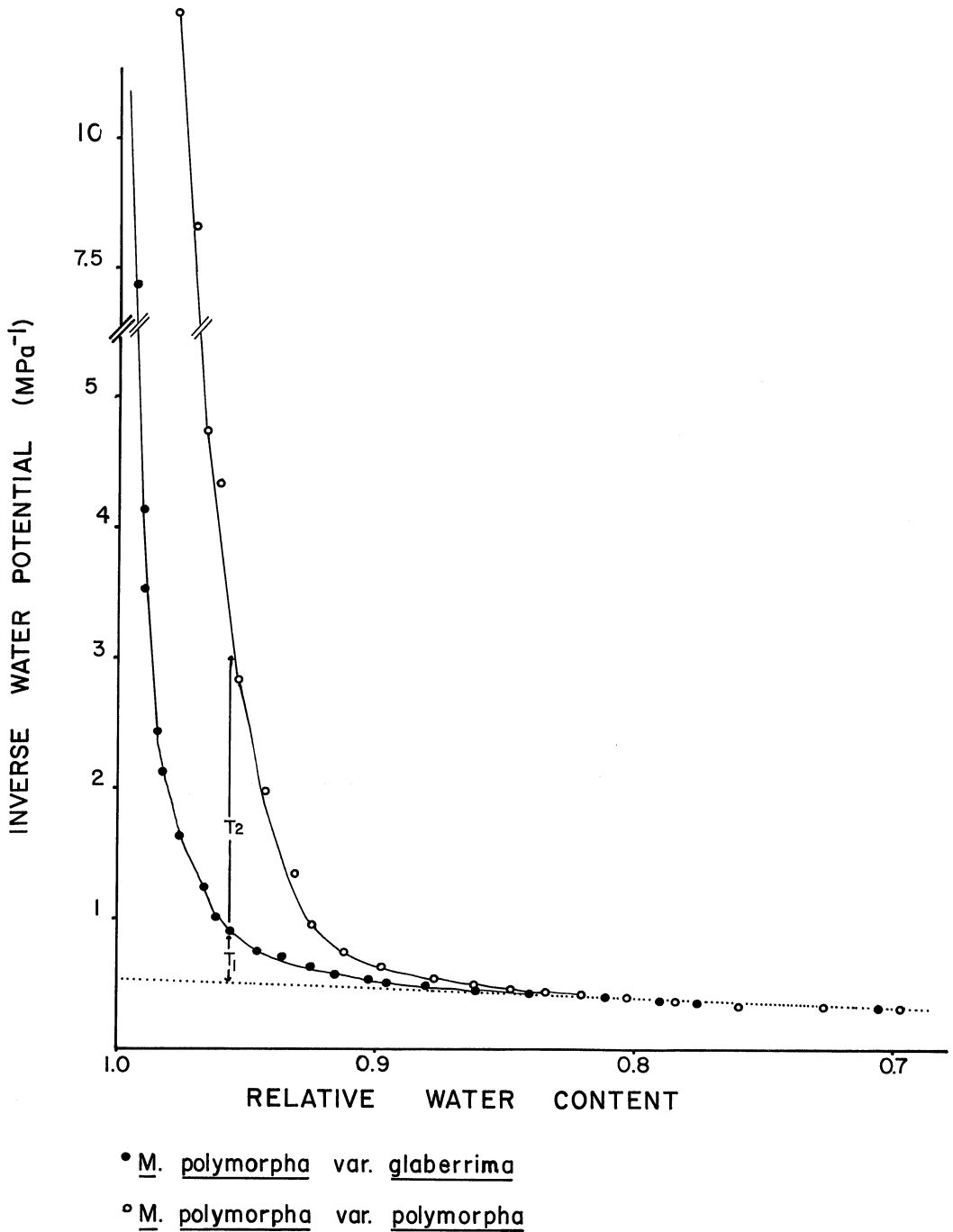
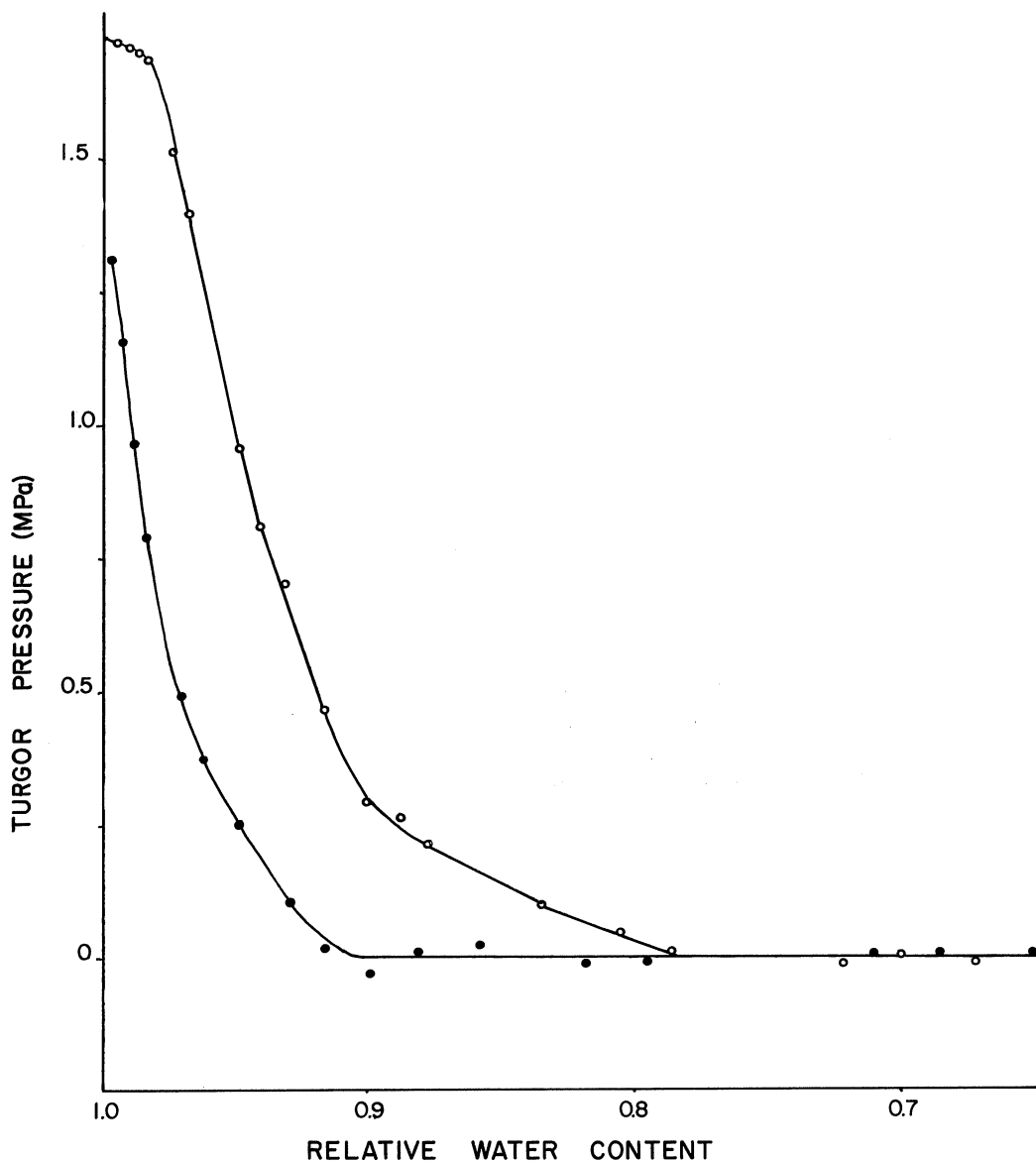


FIGURE 4. Representative pressure-volume curves of adjacent trees on the 1855 lava flow along the Wailuku River Road. Note that the x axis is labeled so that saturation, where relative water content is 1.0, is on the left side, with progressively lower relative water contents indicated toward the right. Extrapolation of the linear portion of the curve to the y axis gives an estimate of the inverse osmotic potential at full turgor. In this example, the osmotic potentials of the two samples are similar, being  $-1.874$  MPa for *M. polymorpha* var. *glaberrima* and  $-1.826$  MPa for *M. polymorpha* var. *polymorpha*. The difference between the line defining the reciprocal of osmotic potential and the inverse of observed water potential gives an estimate of turgor. Note that turgor at 0.955 relative water content for the glabrous *M. polymorpha* var. *glaberrima* is  $T_1$ , which is less than that for a neighboring pubescent variety *M. polymorpha* var. *polymorpha* with a turgor of  $T_1 + T_2$ . Additional nonplotted points at relative water contents less than 0.7 fall on the linear portion of the curve, and additional nonplotted points of inverse water potential are greater than 10.



● *M. polymorpha* var. *macrophylla*

○ *M. polymorpha* var. *incana*

FIGURE 5. Comparison of turgor versus relative water content between the pubescent *Metrosideros polymorpha* var. *incana* growing as a pioneer on the 1955 flow near Pāhoa and the glabrous *M. polymorpha* var. *macrophylla* growing in an adjacent tall canopy forest (see Figure 1, Table 1). Osmotic potential at full turgor is  $-1.346$  MPa for the glabrous 'ōhi'a in the successional advanced forest and  $-1.728$  MPa for the 'ōhi'a on the recent lava flow. The bulk modulus of elasticity is  $27.786$  MPa for the glabrous 'ōhi'a and  $3.234$  MPa for the pubescent sample. Note that the pioneer *M. polymorpha* var. *incana* retains turgor at lower relative water contents than *M. polymorpha* var. *macrophylla*.

where  $P$  is turgor pressure,  $RWC$  is relative water content, and  $A$  is the apoplastic water content. Low values are indicative of resistance to turgor loss as relative water content decreases. Low bulk moduli of elasticity and relatively negative osmotic potentials both allow for turgor maintenance with decreasing relative water content. Therefore, plants able to maintain turgor as relative water content decreases are likely to retain turgor-dependent processes such as stomatal opening, protein synthesis, and cell wall extension under those conditions (Hsiao et al. 1976).

When graphs such as Figures 4 and 5 are compared for 'ōhi'a from adjacent sites on young and old substrates, the osmotic potentials of the pubescent plants in the pioneer stands tend to be relatively more negative than those of glabrous 'ōhi'a in adjacent older forests, and the bulk moduli of elasticity also tend to be lower. Both these traits permit turgor maintenance under relatively dry conditions that would be characteristic of recent lava compared with the more mesic conditions of a rain forest. In the example presented in Figure 5, the osmotic potential at full turgor for the pioneer *M. polymorpha* var. *incana* is  $-1.728$  MPa, and  $-1.346$  MPa for the older forest *M. polymorpha* var. *macrophylla*. The bulk moduli of elasticity are  $3.234$  MPa and  $27.786$  MPa, respectively. These differences are also apparent when the two varieties grow side-by-side on the same substrate, as in the example shown in Figure 4. Here, the osmotic potentials are  $-1.874$  MPa for *M. polymorpha* var. *glaberrima* and  $-1.826$  MPa for *M. polymorpha* var. *polymorpha* and the bulk moduli of elasticity are  $26.276$  MPa and  $7.368$  MPa, respectively. Although osmotic potentials at full turgor are similar in this example, differences in the bulk moduli of elasticity tend to differ consistently between the pubescent and glabrous varieties.

In the rain forest zone, one 'ōhi'a variety appears to replace another in primary succession. When curves from 'ōhi'a growing in an extremely dry site are compared with those from 'ōhi'a growing in a wet rain forest, considerable differences are seen in the ability of the two to maintain turgor. Outside the

rain forest in seasonally dry environments, 'ōhi'a is present in pioneer situations, but may be absent from older successional stages. There, 'ōhi'a is largely replaced by other species such as *Acacia koa*, *Sophora chrysophylla*, *Myoporum sandwicensis*, *Diospyros ferrea*, *Osmanthus sandwicensis*, and *Dodonaea* spp., among others. For example, the upper tree line vegetation on the east flank of the volcanically young Mauna Loa is comprised mostly of *Metrosideros polymorpha*, while on the older Mauna Kea, *S. chrysophylla* is the dominant tree line species (Mueller-Dombois and Krajina 1968). As another example, Rock (1913) describes the diverse and unique vegetation of the lowland dry, or xerophilous, forest on old 'a'ā flows of Kapu'a and Pu'uwa'awa'a, which are dominated by *Diospyros* and *Osmanthus*, and mentions that *Metrosideros* forms almost pure stands on lava flows of more recent origin in these areas.

#### CONCLUSIONS

It has been documented that certain 'ōhi'a taxa are characteristically pioneers on recent substrates, and others are components of forests on older substrates. The differences among them have been demonstrated to be genetically based, and there are physiological differences between the two types in terms of their water relations. While present work was concentrated on the water relations of different 'ōhi'a, it is also likely that selection and evolution has led to physiological and morphological adaptations to other aspects of the microclimate (including water, nutrient, and light availability) associated with the seral stages following the initial colonization of recent volcanic sites.

Recognition of the successional position of different 'ōhi'a varieties has supported the developing theory that the widespread dieback on the island of Hawai'i is part of a successional process. A physiological similarity among dieback trees in a stand, as implied by the theory of cohort senescence, and climatically, geologically, or other environmentally mediated stress that might occur

across a common substrate, could all contribute to the observed dieback synchronicity of canopy trees.

While this study has been concerned primarily with differences between pioneer 'ōhi'a and 'ōhi'a in nearby forests on older soils, the nature of volcanic islands is such that they are ever-changing and continually producing new local environments. It is likely, too, that different kinds of 'ōhi'a are consequently replacing each other along with these changes. Taxonomically, *Metrosideros* species in Hawai'i have been thought to have evolved from a single introduction (Fosberg 1948). However, the consistency of habitat and morphological differences noted between the group of *Metrosideros* from dry sites and those from wetter situations suggest an alternative hypothesis—that there was more than one introduction, and that evolution may have occurred along more than one line.

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